Differential Seed Predation on Two Species
of *Arctostaphylos* (Ericaceae)

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Summary. The fire-prone California chaparral contains two sympatric species of shrubs: *Arctostaphylos glauca* and *A. glandulosa*. A previous study showed that in a stand where both species had similar amounts of coverage, *A. glauca* had fewer seeds in the soil. We attempt to answer the questions: 1) Could ground-foraging seed predators produce the lower population of *A. glauca* seeds in the soil? 2) Do predators select fruits randomly with respect to fruit size? 3) Do the fruits of the two species differ in the proportions of fruit components (i.e. seeds, endocarp, mesocarp, and exocarp) in ways that could be important to seed predators? Predation was measured on artificial caches of fruits, for 17 weeks. Selection by predators was examined by comparing weights of fruits recovered from soil samples with newly-matured fruits on the shrubs. Fruits components were characterized by dividing fruits into 3 fractions and weighing. More fruits of *A. glauca* were removed from the caches. Fruits of both species recovered from the soil were lighter than those on the shrubs. The weights of seeds, stony and fleshy fruit layers were all larger in *A. glauca*. Within fruits of *A. glandulosa*, the weights of the three components, various combinations, and ratios were all significantly correlated, while in *A. glauca* no other component, combination of components, or ratio examined was significantly correlated with the weights of the seeds.

Introduction

The California chaparral is predominately an evergreen sclerophyllous-leaved scrub vegetation adapted to that region's climate of mild wet winters and dry summers. Concomitant with the long summer droughts are frequent fires. Adaptation to fire is evidenced by these shrubs' rapid recovery after fire, either

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by sprouts from below ground vegetative parts or by the abundant production of seedlings. In fact, the seeds of many species germinate only after fire. Although some shrub species re-establish by both means equally well, others rely almost entirely on one or the other of these methods. For example, in the genus *Arctostaphylos* it is well known that after fire the nonsprouting *A. glauca* Lindl. produces large numbers of seedlings and the sprouting *A. glandulosa* Eastw. produces few seedlings (Jepson, 1916, 1939; Horton and Kraebel, 1955; Plumb, 1961; Wells, 1962, 1969; Hanes, 1971). Greater seed production by *A. glauca* was thought by some of these authors to account for the greater seedling number. This view assumes that seedling density is directly dependent on a shrub's relative production of seeds.

Recently in a mature stand of chaparral, Keeley (1973) found seed populations in the soil which are inconsistent with this view. In this study, soil samples were taken from an area with nearly equal values of relative dominance of both of these species. The soil samples contained over 25 times more *A. glandulosa* propagules than *A. glauca* propagules. Since the fruits of the former species break into several segments consisting of one to many fused nutlets (achenes), whereas *A. glauca* fruits remain intact (Fig. 1), this is not a direct reflection of the differences in numbers of fruits in the soil. However, dividing the number of *A. glandulosa* propagules in the soil by the average number of segments per fruit for that species (3.8, Keeley, 1973) shows that *A. glandulosa* had a greater (7 times) number of fruits in the soil than *A. glauca*. An adjacent burned area, which had a relatively similar density of *Arctostaphylos* shrubs prior to the fire, had qualitatively similar numbers of seedlings as those reported by the above authors (8,500/ha for *A. glauca* and 1,050/ha for *A. glandulosa*). These two facts indicate that the production of more seedlings by *A. glauca* after fire may not be explained simply by greater fruit production by that species.
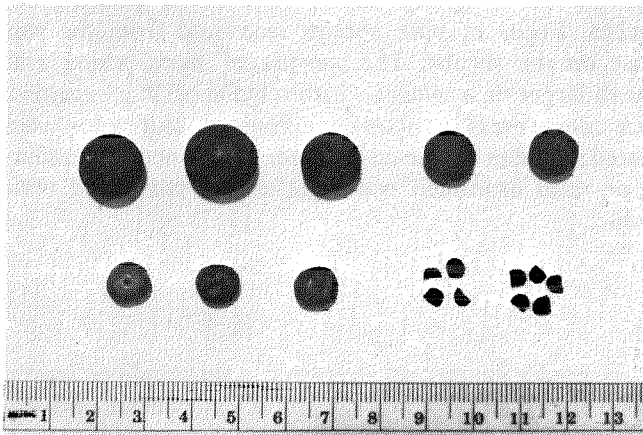

Fig. 1. Fruits of *Arctostaphylos glauca* (top row) and *A. glandulosa* (bottom row). The three fruits on the left (both rows) have the outer exocarp intact. Once the fruits fall from the shrub, the exocarp and mesocarp are soon lost leaving the seeds protected by only the hard resinous endocarp (the two fruits on the right). The ruler is in mm

This discrepancy between seed production, seed populations in the soil, and seedling production raises two questions: 1) If *A. glauca* typically produces more fruits than *A. glandulosa*, how does one account for the greater abundance of *A. glandulosa* fruits in the soil? 2) If *A. glandulosa* propagules are the most numerous in the soil prior to a fire, how does one account for the much greater numbers of *A. glauca* seedlings after a fire? This investigation will focus on the first question.

The importance of seed predators in reducing the seed population actually available to germinate has been stressed by recent workers (for review, see Janzen, 1971). *Arctostaphylos* fruits are an important source of food for certain rodents common in the chaparral; kangaroo rats, *Dipodomys heermanii* (Smith, 1942), and deer mice, *Peromyscus maniculatus* and *P. boylei* (Jameson, 1952). They are also known to be eaten by woodrats, *Neotoma fuscipes*.(Horton and Wright, 1945), rabbits, *Sylvilagus bachman* (W.E. Glanz, pers. comm.), and coyotes, *Canis latrans*. Can these predators account for the anomalous densities of seeds in the soil? Do they exert selective pressure favoring fruits with particular characteristics within each species?

We hypothesized that where both species of *Arctostaphylos* occur together, there is greater predation on *A. glauca* fruits. Our prediction was that if caches of fruits of both species were made at the site studied by Keeley (1973), then a greater percent of *A. glauca* fruits would be destroyed or removed. No attempt was made in this study to determine the amount of seed predation prior to the fruits dropping to the ground nor to determine the animals involved in predation. As a possible indirect measure of predation effects, newly produced fruits were compared with fruits stored in the soil.

If predation is significant on the fruits of *Arctostaphylos* then one would expect that the more heavily utilized species would respond evolutionarily to decrease this loss. This might be reflected, for example, in a greater allocation of resources to tissues attractive to dispersers, or those furnishing protection to the seeds. What differences exist within and between species in fruit characteristics? How are these related to dispersal and predation?

Study Site and Methods

This study was carried out at the same site from which the soil samples were taken by Keeley (1973). It was located approximately 10 km south of Interstate Highway 8, at the junction of Japatul-Lyons Valley Road and Lawson Truck Trail (elevation 675 m), San Diego County, California.

The area was approximately half a hectare covered by very old chaparral shrubs which had not burned for more than 90 years, surrounded by chaparral that had burned more recently. The dominant species were: *Actostaphylos glauca, A. glandulosa, Adenostoma fasciculatum* H. and A., *Quercus dumosa* Nutt., and *Ceanothus greggii* Gray var. *perplexans* (Trel.) Jeps. The species studied, *A. glauca* and *A. glandulosa*, were nearly equal in relative dominance, based upon the basal area of live stems (33.2 and 32.2, respectively, Keeley, 1973).

The prediction that predation on *A. glauca* seeds would be greater than on *A. glandulosa* was tested as follows. Fifteen shrubs of each *Arctostaphylos* species were randomly selected. Under each shrub 20 fruits of that species were placed in a pile on the ground in an area of about 2 dm^2 from which the litter was removed. The litter was of variable depth of up to about 4 cm.

Each week from April 21 to May 25, 1973, then every other week from June 6 to August 4 the number of fruits destroyed or missing was recorded. Fruits of *A. glandulosa* which were broken into fragments were scored by converting the number of apparently undamaged nutlets into the equivalent number of whole fruits. This was done by dividing by the average number of segments per fruit, and rounding to the nearest whole fruit. Fruits removed or destroyed were replaced by whole ones.

The low fruit production in 1973 (*A. glauca* produced only 1.6 fruits/m^2 of areal coverage and *A. glandulosa* did not fruit at all) essentially precluded errors resulting from fruits failling into the caches.

As a test of selection by predators, a comparison was made between the weights of fruits in the soil and newly produced ones still on the shrubs. Those from the soil included all propagules of *A. glauca* recovered in the soil samples and all the propagules of a single soil sample of *A. glandulosa* used by Keeley (1973).

Fresh material was collected from the fruit crops of 1972 and 1974 from this site using the following procedure. A line transect was randomly laid out on the site. The first 15 shrubs of each species encountered were sampled. All fruits from one quarter of each shrub were removed. Fruits from each species were combined in a bag, shaken and a subsample was taken. The exocarps and mesocarps were removed from the fruits of the recent crops since they had already been lost from the fruits in the soil. The *A. glandulosa* fruits were rubbed vigorously on a screen so they would break into segments. All propagules were oven dried to constant weight and weighed.

To characterize the sizes of the components of the fruits, 25 from each species were taken from the sample of the 1974 crop on the shrubs. These were divided into three components: Exocarp plus the powdery mesocarp, the resinous endocarp, and the seed. These were oven dried to constant weight and weighed.

Results

The percentage of fruits removed from caches over the eleven sampling intervals from April 21 to August 4 are shown in Figure 2 and compared statistically in Table 1. The variance of the number removed was calculated separately for each interval and each species. These were found to be non-homogeneous by the *F*-max test. The mean number of fruits removed from the caches of each species were compared with the Wilcoxon's Signed Ranks test using the means for a given date as a pair. The null hypothesis was rejected with $P < 0.05$, indicating that predation was significantly higher on *A. glauca*.
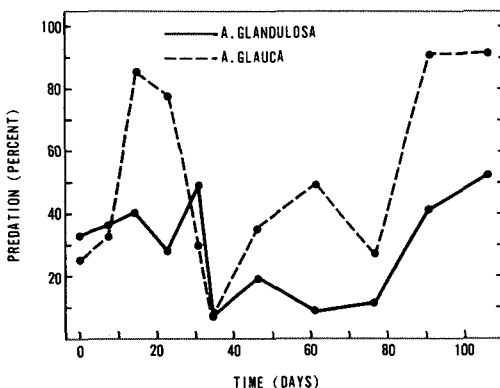

Fig. 2. The percentage of fruits removed from caches of twenty each, for eleven sampling periods (day 0 is April 7, 1973)

Table 1. The number of fruits removed from artificial caches of twenty each, for eleven sampling periods

	A. glauca	A. glandulosa
Mean number removed per period	10.1*	6.0*
Standard deviation	8.0	6.9

* Significantly different, $P < 0.05$

Table 2. Comparison of propagule oven dry weights (minus exocarp and mesocarp) between those in the soil and those of crops still on the shrub

	Soil	1972	1974
Arctostaphylos glauca			
Mean (mg)	308	508 N.S.	506 N.S.
Variance	26,000	52,000	33,000
Number of fruits	118	101	250
A. glandulosa			
Mean (mg)	9	16	22
Variance	130	270 N.S.	260 N.S.
Number of fruits	302	130	250

All means and variances are highly significantly different, $P < 0.01$, except those pairs labeled N.S., $P > 0.05$

The mean number of fruits removed from the caches was highly variable for both species (Table 1). The mean number of *A. glauca* fruits removed during a given period was positively correlated with that of *A. glandulosa* (Spearman's Rank Correlation, $r_s = 0.545$, $P < 0.05$ that $r_s < 0$).

The results of a comparison between the propagules in the soil and those of the current year's crop removed from the shrub are given in Table 2. The variances of the oven dry weights of the propagules (minus exocarps and mesocarps) within each species were compared with the F-test. The means were compared using the *t*-test. Where the variances were homogeneous the usual method involving the calculation of the pooled standard error was used. Where the variances were not homogeneous, the method used was that described by Dixon and Massey (1969) for this case. In general, each sample differed significantly from the others of the same species. The only parameters which were not significantly different were the variances of the 1972 and 1974 samples from the shrubs of *A. glandulosa*, and the means of the 1972 and 1974 samples from the shrubs of *A. glauca*. In each case the propagule samples from the soil were less variable, and had lower means than those from the shrubs. There was no consistent pattern between the species in the differences between the 1972 and 1974 samples from the shrubs.

The oven dry weights of the fruit components (exocarp, endocarp, and seed) are summarized in Table 3. For each component, the distributions of the species do not overlap. *A. glauca* is larger in all cases. The ratio of endocarp

Table 3. The oven dry weights of the fruit components for both *Arctostaphylos* species

Component	Parameter	A. glauca	A. glandulosa
	Number analyzed	25	25
Total fruit	Mean (mg)	1,006***	124***
	S^2	26,400***	2,470***
	Coef. of var. (C.V., %)	16.2	40.1
Exocarp plus mesocarp	Mean (mg)	239***	47***
	% of total	23.8***	37.7***
	S^2	1,700***	422***
	C.V.	17.2	43.9
Endocarp	Mean (mg)	718***	68***
	% of total	71.4***	55.2***
	S^2	15,400***	769***
	C.V.	17.3	40.5
Seeds	Mean (mg)	48***	9***
	% of total	4.8^N.S.	7.2^N.S.
	S^2	137***	7***
	C.V.	24.2	30.1
Endocarp/seeds	Mean	15.6***	7.8***
	S^2	17.6	4.54
	C.V.	26.8	27.4

*** Significantly different, $P < 0.001$

Table 4. Correlations between the weights of various fruit components in *Arctostaphylos glauca* and *A. glandulosa* ($N = 25$ for each species. $r = $ Pearson product-moment coefficient of correlation. $P = $ probability that $r = 0$. The equation for the principal axis is given by $Y_g = a + bX_g$)

Variable		A. glauca				A. glandulosa			
Y	X	r	P	a	b	r	P	a	b
Endocarp	Exocarp	0.86	<0.001	− 0.10	3.41	0.94	<0.001	0.00	1.38
Endocarp	Seeds	0.10	>0.50	−	−	0.78	<0.001	−0.05	13.28
Exocarp	Seeds	0.11	>0.50	−	−	0.82	<0.001	−0.04	9.30
Whole fruit	Seeds	0.17	<0.50	−	−	0.83	<0.001	−0.07	22.42
Endocarp + seeds	Exocarp	0.86	<0.001	− 0.06	3.46	0.94	<0.001	0.01	1.49
Endocarp/seeds	Whole fruit	0.37	<0.10	− 54.56	69.78	0.47	<0.02	−3.47	90.50
Endocarp + seeds	Whole fruit	0.99	<0.001	− 0.01	0.77	0.99	<0.001	0.00	0.60
Endocarp + seeds	Seeds	0.19	<0.50	−	−	0.82	<0.001	−0.04	13.68
Endocarp/seeds	Endocarp + seeds	0.35	<0.10	− 57.20	95.03	0.52	<0.01	−2.89	137.68
Exocarp	Whole fruit	0.92	<0.001	0.00	0.23	0.98	<0.001	0.00	0.41

to seeds was calculated for each fruit (Table 3). The species' distributions for this parameter did overlap, but the null hypothesis was rejected (Mann-Whitney U Test, $P \ll 0.001$ that *A. glauca = A. glandulosa*).

Since our results indicate that heavier fruits (minus exocarps) were preferentially removed, we subjected the weights of the components of fruits to correla-

tion analysis. Table 4 gives the results, including the Pearson Product-Moment Correlation Coefficient, and the coefficients of the equation for the principal axis. Scatter diagrams were prepared for those correlations found to be significant ($\alpha < 0.05$ that $r = 0$). No large deviations from an eliptical pattern were noted. All correlations in *A. glandulosa* were significant and positive. In *A. glauca* the weight of the seeds was not significantly correlated with either of the other two components, or with the weight of the whole fruit. The weight of the endocarp is significantly correlated with that of the mesocarp plus exocarp. The endocarp plus seeds is significantly correlated with the mesocarp plus exocarp, and with the weight of the whole fruit. The ratio of the endocarp to the seeds is weakly ($0.10 < P < 0.05$) correlated with the weight of the whole fruit, and with the weight of the endocarp plus seeds.

Discussion

In the stand of chaparral studied, *Arctostaphylos glauca* fruits are removed from caches about 1.7 times more frequently than are those of *A. glandulosa*. Can this value be applied to the loss of fruits between the shrub and the soil, and from the soil itself? This would require that two main assumptions be met. The first is that the fruits removed were destroyed. The fruits of both species have a mealy mesocarp surrounded by a fairly thin exocarp. When ripe, the fruits are moderately conspicuous to the eye. They are reddish brown, and contrast with the grey-green foliage. They have no conspicuous odor. After ripening they remain on the plant for a time, but eventually fall to the ground, where they can accumulate in large numbers. These characteristics suggest that dispersal of fruits directly from the shrubs by large mammals or birds is important. This is supported by the common occurrence at certain times of coyote scat that consists almost entirely of *A. glauca* fruits. The endocarps are intact, suggesting that the seeds remain viable.

It is possible that some fruits were removed from the caches and the unharmed seeds deposited in the area in feces, animal caches, etc. This could not have occurred very commonly, however, since in all cases where several fruits were missing, the cache sites were littered with fragments of endocarps, exocarps, and mesocarps. This suggests that most seeds were consumed in situ, which is further supported by the observation of numerous rabbit feces on and near caches from which substantial numbers of fruits were removed. The lack of data on the removal of fruits directly from the shrubs limits the extent to which ground-dwelling seed predators can be held solely responsible for the anomalous densities of fruits in the soil.

The second assumption which needs to be met is that the activities of animals are similar for fruits in caches and those deposited naturally into the litter. One might expect that handling the fruits and depositing them in piles in small clearings would result in unusual responses. There are no data bearing on this point. We doubt, however, that there would be substantial differences in the responses to the fruits of the two species resulting from these factors.

Could the rates of fruit removal observed account for the anomalous densities of seeds in the soil? We divided the mean proportion of fruits of a species removed in each period by the number of days since the cache was last replenished. We them calculated the means for each species, which gave 0.053/day for *A. glauca* and 0.033/day for *A. glandulosa*. We then assumed that over longer periods the number of fruits remaining follows an exponential decline. Starting with equal numbers of fruits for each species, the ratio of 1 to 7, which was found in the soil, would occur in 108 days. At this time 0.4% of the *A. glauca* fruits would remain. Data are inadequate to test the accuracy of this prediction for natural removal of fruits. For example, Keeley's (1973 and unpublished) comparison of fruits in the soil and production by the shrubs indicated that the population of *A. glauca* fruits in the soil was 1.02×10^6 fruits/ha, while annual production was 0.021, 0.009, 1.9 and 0×10^6 in 1972, '73, '74, '75, respectively. This variability precludes meaningful comparisons with the rate of loss from the caches. In addition, this variability in fruit production may influence the behavior of the seed removers. The relative rates calculated might not be the same from year to year.

The results of the comparison of fruits collected from the shrubs and those recovered from the soil indicate a definite preferential removal of fruits with a large total weight of endocarp and seeds within each species. This could be due to 1) a direct perception of that weight by a seed predator. On the other hand, these results could also be explained by two other hypotheses.

2) The animals could prefer heavy whole fruits, and as a consequence remove those with a heavy sum of endocarp and seeds. This is supported by the strong correlation in each species between the weight of endocarp plus seeds and that of the whole fruit (Table 4).

3) Finally, the animals could prefer fruits with a heavy sum of exocarp plus mealy mesocarp, and as a consequence remove those with a heavy sum of endocarp plus seeds. This is supported by the strong correlation in each species between these components (Table 4). On the other hand, the presence of large quantities of fragments of endocarps, exocarps, and mesocarps but not seeds in the caches suggests that the seeds, and not the exocarps or mesocarps, were being eaten. All three of these hypotheses are also supported by the preference by animals for *A. glauca* over *A. glandulosa* since the former species had fruits with greater total weight, and greater weights of each component (Table 3). We conclude that there is not enough data to reject any of these hypotheses but that hypothesis three has the weakest support.

If we conclude: 1) that predation of *A. glauca* fruits is greater than that of *A. glandulosa* fruits and 2) that fruits with larger total weight are preferred by animals, then the question arises of why.

Current theory on food selection in herbivores has three major components: search cost; handling cost; and energic reward. The fruit characteristics of *A. glauca* and *A. glandulosa* vary with respect to these components (Fig. 3). Because the latter species' fruits are smaller (Table 3) and easily break up into smaller fragments, they are much harder to find and yield less energy (seed weight, Table 3). However, they presumably require less handling time (endocarp weight, Table 3). The propagules of *A. glauca* on the other hand require less
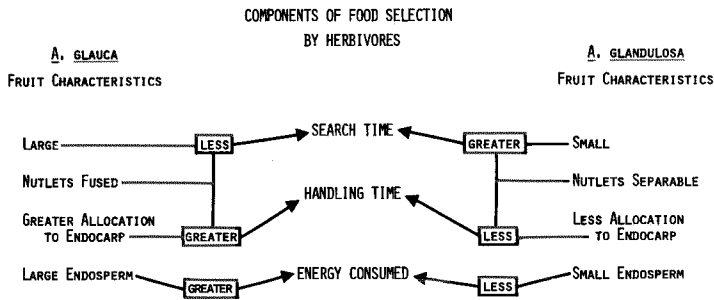
COMPONENTS OF FOOD SELECTION
BY HERBIVORES

A. GLAUCA   A. GLANDULOSA
FRUIT CHARACTERISTICS   FRUIT CHARACTERISTICS

LARGE —————————[LESS]——→ SEARCH TIME ←——[GREATER]——— SMALL

NUTLETS FUSED ——————————| |———————— NUTLETS SEPARABLE

                        HANDLING TIME

GREATER ALLOCATION   LESS ALLOCATION
  TO ENDOCARP ————[GREATER]   [LESS]—————— TO ENDOCARP

LARGE ENDOSPERM ——[GREATER]——→ ENERGY CONSUMED ←——[LESS]—— SMALL ENDOSPERM

Fig. 3. Fruit characteristics of the two *Arctostaphylos* species in relation to components of food selection by herbivores

search time due to their large size and yield a greater energy source while requiring a greater handling time. In this stand of chaparral it appears as though evolution has favored the ground dwelling seed predators which take the largest seeds. It is possible these results merely represent the absence in this stand of chaparral of "the predator" adapted to this smaller seed type (Brown and Lieberman, 1973). However, our results are consistent with those of Rosenzweig and Stener (1970) and Smigel and Rosenzweig (1974) who have shown that based on laboratory measurements of husking speed, each species ought to eat the largest seeds it can find.

If the predators prefer *A. glauca* fruits, then are there any advantages to the size and morphology of these fruits? The characteristic of entirely fused nutlets with a very hard resinous endocarp is found in only about six out of the 50 or so species in the genus (Wells, 1972). All of these species are found in the chaparral scrub of southern California and Baja California, although the genus ranges from Central America to the Arctic.

Wells (1972) has suggested that this type of seed morphology is an adaptation which arose in response to fire. This would in part be supported by the hypothesis that the southern California region has had the mediterranean climate longer than other parts of California, and presumably has had a longer exposure to frequent summer fires than other parts of western North America (Axelrod, 1973). How then does one sort out the effects of fire and predation on selection of seed characteristics? Smith (1970) has confronted this problem in dealing with serotinous cones and predation by squirrels. He has assumed that the chain of selective pressures started with the frequency of fires and thus led to serotinous cones, then to increased selective pressure from squirrels for hard cones with fewer seeds which finally selects for squirrels with stronger jaws.

It is likely that a similar sequence has occurred in *Arctostaphylos*. A model of how this may have occurred is as follows. Since *A. glauca* is a nonsprouting shrub, selection would tend to favor those individuals who could re-establish with the greatest probability following fire. Thus, there would tend to be selection for larger amounts of endosperm allocated to the seedling. This would result in a more highly prized and easily found reward for a predator as well as resulting in decreased numbers of fruits (Janzen, 1969) and decreased dispersa-

bility of fruits (Salisbury, 1942; Wells, 1962; Baker, 1972). The increased seed predation along with the decreased number and decreased dispersability would result in a decreased chance of reaching a safe site for germination (Harper et al., 1965) particularly safety from being destroyed by fire. It is likely that seed predation and destruction by fire have interacted in selecting for increased protection of the larger endosperm investment. This is supported by the larger ratio of endocarp to seeds in *A. glauca* and the large positive slope of the correlation between this ratio and both, the whole fruit, and the weight of the sum of endocarp and seeds, in *A. glandulosa* and perhaps in *A. glauca*. The greater weight of the exocarps and mesocarps in fruits of *A. glauca* might be due to an increased investment in characteristics that would encourage dispersal by birds, etc., or as protection against the numerous insect predators on developing fruits. However, the proportion of the fruit weight in these components is smaller than in *A. glandulosa*. The increases in both the exocarp plus mesocarp and the endocarp should increase the number of fruits which reach safe sites. In addition this protective endocarp would decrease the number of fruits destroyed by fire, thus increasing the number of sites safe from fire.

While competitive ability following germination, plus protection from fire may select for larger fruits, predation appears to select for smaller fruits. Although seed predation has been shown in this study to have the potential for shaping seed characteristics whether it actually does so to a significant extent remains to be demonstrated. This caution is particularly wise in light of the estimate that over 99% of the *A. glauca* propagules in the soil do not produce seedlings after fire (Keeley, 1973). This indicates a very highly buffered population of seeds exists in the soil.

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